Plant growth regulator

Are organic compounds other than nutrients, which in small amounts promote, inhibit, or otherwise modify any physiological process.

Are regulator produced by plants, which in low conc one regule plant physiological process. Hormon move within the plant from a site of production to action.

are regulators that affect growth.

Thimann (1934) in his determination of the auxin content in different areas of the Arema seedling (Figure 17-2). The cop centration of auxin drops as one pro grosses from the tip to the base of the colcoptile, the highest content being found at the tip and the lowest at the base. Con timing from the base of the coleoptile along the root, there is a steady increase in auxin content until a high point is reached at the tip of the root. The concentration of auxin found at the tip of the root is, how ever, nowhere near the concentration found at the tip of the coleoptile. Since Thimann's early work, several studies on auxin distribution have been made roughly confirming the widespread occurrence of auxin in the plant him and Slay 1934; an Oi k dal., 1947).

Thiman's work on the distribution of

in, and later the work of others, disclosed that auxin is present in the plant in two different forms, one that is easily ex tracted by diffusion cthods and another that is

much more dillicult to extract, necessitating the use of organic solvents The easily extracted in is called five

and that which hard to extract band . It is now cally accepted des bound in is the form that is active in growth and that free Bus O SS uxin in equilibrium with the bound auxin.

Yet a third form of aukin has been postu basipetal has been criticized by Jacobs lated Audies, 1959) that requires more (1961). He found that in Colens stem se drastic cares for removal from plant ions the ratio of basipeal to acropetal material than simple diffusion methods are to tip) transport of auxin is 3:1. direct extraction with some organic sol Although crop tal movement is only one vent. For example, spinach leaves heated third that of basipetal movement, it is in weak alkaline solution or treated with real and significant. Also, some of the auxin chrymes that break up protein where produced by leaves is transported in the ausin may be bound) giveup a much higher phloem tisto odier parts of the plant content of auxin than would have been (Andes, 1959), a type of transport that is found if only direct extraction procedures definitely mor polar. Finally, in recent had been performed. It would appear, then studies Golemi, 1956, 1967; Lime and that auxin may be found in the plant in two Gold , 1967) Goldsmith has clearly or more active forms, posibly forming shown that auxim movement occurs acrodifferent protein complexes.

petally as well as basically, although hasi So far, it has been suested that auxin petal movement is strongly favored. in the plant is present in a free nonactive The translocation of anxin in plant tissues form and a "bound" active form, and that occurs at such high rates as to exclude a dynamic equilibrium exists between the diffusion as the principal method of auxin two. There may be several different forms transport. Also in favor of a method other of the bound auxin. Oman conclude from a diffusion or in addition to diffusion the above information that growth, its - Esthe fact that ausin in the plant can move initiation and regulation may be controlled painst a concentration dent. Velocities by the conditions of different equilibria for auxin transport recorded in the litera between free and bound auxin a various tue vary with the type of plant being growth centers in the plant. Most likely, studied and the conditions under which auxim is transported in the free form from experiments were performed. Thus, vel its place of origin to its site of activity. cities anywhere from 64 mm/hour to

26 mm/hou have been observed it,

1965; 1965; Rajal, 1967). Translocation of Auxin

The actual mechanism involved in the

transport of anxin is still a matter of con The translocation of auxin in plants is a troversy. One group of investigators be subject that plant physiologists have occu- lieves that difference in dectrical potential pied themselves with for many years and between the tip and the use of the coleope have not completely solved. Experimentsile controls ausin trong Land, 1947 by Darwin and lvy Boy -Jensen (sce Sdna, 1951). "The base of the Avg p. 306) demonstrate the movement of colcotile is more electropositive than the an active stimulus from the tip to the base tip, the dark side of a unilaterally illumiof the coleoptile, led other investigators to mated coleoptile is more electropositive

me that the movement of this stimulus than the lehted side, and in a horizontally war polar. Experiments by Went (1928) placed coleoptile the lower side is more and Beyer (1928) carly in the study of auxin clectropositive. In cach of these situations supported this concept and for many years the translocation of auxin is toward the auxin movement in the plant was believed highest positive charge. One very serious to be strictly polar. This movement was objection to this theory, however, is that thought to occur in a basical direction: when a transverse External field is applied that is from top to base.

to the coleopt ike, initial curvature is toward That the transport of a n is strictly the positive pole of the applied charge 8. An w are compounds which inthe plant can be converted into auxins. 9. Are compounds that inhibit competitively the action of

Distribution of Auxin in the Plant

The highest concentrations of auxin are found in the growing up of the plant, that is, in the tip of the coleoptile, in buds, and in the growing tips of leaves and roots However, axin is also found widely distributed throughout the plant, undoubted ly transported from the meristematic re gions. This was clearly illustrated by

(Air V. T 1934 G Pasi 18:23 Rew from A. Leopold 1955 Aplant growth. Li ity of California Pro Los Angeles

Physiological Effects

Since the discovery of auxin and its identification as a growth hormone, an enormous amount of literature has accumulated describing its effect on the growth of the plant. In some cases auxin is stimulatory, in others

0

Time hours

IAA

17-3 Comparison of the effect of aerobic () and anaerobic (

-) conditions on the

total uptake by eat coleoptile sections from either apical or basal donors containing C carboxyllabeled IAA (16-M). (After M. H. M. Goldsmith, 1966. Plant Physiol. 41: 15.)

THE NATURAL GROWTH HORMONES

inhibitory, and in still other cases a necessary participant in the growth activity of another plant hormone (eg, cytokinins and gibberellins). Needless to say, a discussion on all of the physiological aspects of auxin activity is beyond the scope of this book. We will discuss only the involvement of auxin in (a) cell elongation, () phototropism, (c) geotropisni, (d) apical dominance, (c) root initiation, (f) parthenocarpy, (g) abscission, (h) callus formation, and () respiration.

Cell elongation

In an earlier discussion in this book, we studied the osmotic conditions that prevail in the living cell. We learned that the cell membrane and vacuolar membrane are differentially permeable and that osmoti cally active solutes are present in the cell sap and cytoplasm. It was also mentioned that an osmotic equilibrium exists in the cell, where the turgor pressure developed is balanced by an equal and opposite wall

pressure. It is thought that the modification by auxin of the conditions responsible for this equilibrium, such as wall resistance and osmotic concentration, stimulates cell elongation.

Most of the studies of the effects of auxin on cell elongation have employed excised plant material (e.g., cat coleoptile sections or excised root sections) having no endogenous auxin supply. Plant material used in this manner presents an ideal situation for measuring the influence of auxin on cell clongation. The effect of exogenously applied auxin may be measured without fear of any contaminating influence by endogenous auxin.

In a study of IAA-induced cell elongation in oat coleoptile sections, Bonner (1948) found that cell elongation takes place to a small extent in the absence of exogenously applied IAA (Figure 17-4). With the use of competitive inhibitors of 1AA, it was determined that noninduced elongation is

Growth,mm

IMA concentration

2 x 10-M

12

COM

307

10

Time, hours

17-4 Growth of Arene coleoptile sections in an auxin medium and in the absence of maxin. The initial length of the sections was 5.0 mm. (Repro duced from Plant Growth Regulation, edited by R. M. Klein, 1961 by the lowa State University Press)

not due to any residual IAA that might be present in the coleoptile section.

It should also be noted in Figure 17-4 that the response of the coleoptile section to optimal concentrations of LAA is very large, causing in some cases a tenfold increase in rate of elongation over the rate in the absence of IAA (Beer, 1961).

We have already mentioned that the action of auxin on cell elongation must involve some modification of the osmotic system of the cell. How then would this be accomplished? The theories proposed from major studies on this problem have suggested that auxins may (a) increase the esmotic content of the cell, (b) increase permeability of the cell to water, (c) cause a reduction in wall pressure, (d) cause an

increase in wall synthesis, or (e) induce the synthesis of specific RNA and protein (enzymes) which, in turn, lead to an increase in cell wall plasticity and extension.

Increase in osmotic solutes The amount of solute present in the cell sap increases in a cell treated with IAA (Cleland and Burström, 1961). However, the osmotic concentration or concentration of osmotically active solutes does not change (Beck,1941Cleland and Burström, 1961; Galston, 1949) and might even decrease (Hackett, 1952).

Since the osmotic pressure does not increase, it is hard to believe that an auxininduced increase in amount of osmotically active solutes alone is responsible for an increase in cell extension. In fact, the increase in solutes may be an effect rather than the cause of an increase in cell elonga

tion.

However, strong support for osmotic pressure playing a major role in cell clongation has been given by Ordin et al. (1956). They found that oat coleoptile sections failed to respond to IAA treatment when placed in an isotonic solution. Oat coleoptile section growth was found to be quite sensitive, however, if the osmotic pressure of the external solution was dropped below the isotonic condition (Figure 17-5).

Increased permeability to water Northern (1942) observed that auxin decreases the viscosity of cytoplasm, leading him to propose that auxin may bring about the

Growth

1.0

+AA

0.2

04

External concentration, M

06

17-5 Growth of Area coleoptile sections as a fiction of osmotic concentration. Osmotic solutes were made up of sucrose (0.09) and varied amounts of mannitol (After L. Ordin, T. H. Apple white, and J. Bonner. 1956. Plant Physiol. 31:44. Adopted by permission from Plant Gre Regula tion, edited by R, M. Klein, 1961 by low State University Press)

decomposition of cytoplasmic protein. This decomposition would release osmotically active particles into the cytoplasm, raising its osmotic pressure, which in turn would increase the diffusion of water into the cell.

In a recent review (Cleland and Burström, 1961) the suggestion that auxin induces an increase in permeability to water by the cell has been criticized on the grounds that direct measurements of the uptake of isotopically labeled water demonstrate no influence by auxin.

Reduction in wall pressure! We have already discussed that there is an increase in the quantity but not the concentration of osmotically active particles in auxin-treated cells; that is, no change in osmotic pressure or turgor pressure is noted despite quite an increase in cell size. To allow for this, some of the properties of the cell wall must be modified by the action of auxin.

Reduction in wall pressure has received strong support as the method by which auxin induces cell elongation. How this is done is not clearly understood. In the first stages of cell elongation, the cell wall may actually get thinner (Brown and Sutcliffe, 1950), implying a stretching of the cell wall without an accompanying cell wall synthesis. However, at the end of a period of cell elongation the wall in many cases is thicker (Audus, 1959), suggesting that new cell wall material may be synthesized after the initial stages of extension growth.

It has been noted that elastic stretching (reversible stretching) of a cell increases in auxin-treated tissue only if irreversible elongation also occurs (Cleland and Burstrom, 1961). In the absence of elongation auxin has no effect on the elastic properties of the cell wall, implying that the increase in elasticity may be a consequence of cell elongation, not of auxin.

That auxin increases wall plasticity (irreversible stretching) has been convincingly demonstrated with the Arena coleoptile. It has been shown that cell wall plasticity

increases before and during auxin-induced cell elongation (Tagana and Bonner, 1957). It has been proposed that this may be because of the rupturing of Ca bonds in the cell wall. Experimental support for this proposal has been received from studies by Thimann and Schneider (1938) and Cool and Bonner (1957). See Figure 17-6.

Increase in wall synthesis Although new wall synthesis does occur during auxininduced cell elongation, there is no convincing evidence that this is the cause of cell clongation rather than a consequence of it. However, the fact that auxin will increase the rate of respiration suggests an increase in energy output that might be utilized in the synthesis of new wall material. Again, one doesn't know which comes first, the increase in respiration or the increase in cell clongation.

Inducement of specific RNA and protein synthesis Recent studies of auxin-induced cell wall extension strongly suggest that IAA exerts its influence at a point very close to the gene level. There appears to be an intimate relationship between the effects of auxin on nucleic acids and growth, a relationship first suggested by Skoog in 1954. Since that time there have been numerous studies supporting Skoog's sug gestion that the action of auxin in regulating growth is associated with nucleic acid metabolism (Courtney et al., 1967; Key and Shannon, 1964; Masuda et al., 1967; Nooden, 1968).

The fact that exogenously applied IAA can induce the synthesis of new RNA and protein has been demonstrated in a variety of plant tissues. For example, applied IAA has induced RNA and protein synthesis in Rheee leaves (Sacher, 1967), yeast cells (Shimede et al., 1967), gromm pea stem sections (De Hertegh et al., 1965), bean endocarp (Sacher, 1967), and oat coleoptile sections (Masuda et al., 1967). With the use of specific metabolic inhibitors, this activity of IAA has been proven to be associated with auxin-induced cell wall plasticity and extension. Four inhibitors frequently used in this type of study are activourycin D, chloramphenicol, 8-azaguanine, and promycin. All four in one way or another inhibit RNA and protein biosynthesis. Perhaps at this point it would be best to examine a recent study in which metabolic inhibitors were used to clarify the role of IAA in cell expansion.

Inhibitory effect of calcium on LAA-induced growth of a coleoptile sections. Presumably. this is because of calcium increasing cell wall resistance. (After B. Cooil and J. Blommer, 1957. Planta 48: 696. Adopted by permission from Pleat Gr Regulation, edited by R. M. Klein, 1961 by the lowa State University Press.)

Artichoke tuber disks which have been aged for 24 hours in water respond to exogenously applied IAA with a considerable amount of growth. This increase is accompanied by a substantial amount of new RNA and protein synthesis. However, if actinomycin D (50mg/l) or 8-azaguanine (0.8 mM) are added simultaneously with IAA, the effect of the auxin is almost completely negated (Figure 17-7) (Nooden, 1968). The fact that metabolic inhibitors. of RNA and protein biosynthesis completely offset the effect of IAA on artichoke tuber disks certainly suggests that the primary activity of auxin in cell wall extension is associated with nucleic acid metabolism. The same results with the aforementioned inhibitors have been observed in a variety of plant tissues. These findings place the primary influence of auxin very close to the gene level. One attractive theory is that auxin in some way derepresses a repressed gene(s) which, in turn, releases DNA-template for RNA synthesis. The new RNA-presumably mRNA-would then induce the formation of one or more new enzymes which would increase wall plasticity and extension. In at least one study the enzyme cellulase was induced by the application of IAA to pea epicotyl tissue (Fi and Maclachlan, 1967).

All of the cells of a plant contain the complete complement of DNA that is characteristic for that plant. All of the genes are present but not all of them are active at any one time; that is, each individual cell contains a number of active genes and a number of repressed genes. Thus, we find differences among cells containing the same complement of genes (Sommeborn, 1964). A gene may be repressed by its DNA complexing with basic proteins called histones to form nucleohistones. The forma tion and dissociation of such a complex may be nature's way of switching genes on and off. Perhaps auxin in some manner derepresses a gene by uncoupling nucleohistones, releasing active DNA for mRNA synthesis (Figure 17-8).

Phototropism

When a growing plant is illuminated by a unilateral light, it responds by bending toward the light. The bending of the plant is caused by cells elongating on the shaded side at a much greater rate than cells on the illuminated side. This differential growth response of the plant to light, called phototropism, is caused by an unequal distribution of auxin, the higher concentration of the growth hormone being on the shaded side.

17-8 Schematic representation of the release by auxin of DNA-template for mRNA synthesis. Dissociation of nucleohistones (DNAhistone complex) induced by avorin

releases active DNA for mRNA synthesis. The new mRNA, in tum, mediates the synthesis of new protein.

Any study of the plant phototropic system is complicated by the fact that the response varies with the intensity of light. DuBuy and Nuerenbergk (1934) were able to show that the phototropic response of the oat coleoptile to unilateral light over a wide range of intensities amounted to one negative and three positive curvatures (Figure 17-9). Note in Figure 17-9 that if the proper intensity of light is used, the coleoptile can actually be made to bend away from the source of light (negative curvature). In our discussion we will concern ourselves only with the first positive curvature, since it is in this area that most. of the work on phototropism has been

done.

Many attempts have been made to explain why there is a higher concentration of auxin on the shaded side of a unilaterally illuminated coleoptile. This unequal distri bution of auxin could be accomplished by light-induced inactivation of aucin, lateral transport of auxin, or inhibition of basipetal transport of auxin.

Photoinactivation of auxin It is a wellknown fact that IAA does not absorb wavelengths in the visible portion of the spectrum. Yet, when an oat coleoptile is subjected to a unilateral light, it bends

Curvature degrees toward the light. Since the IAA molecule is not involved directly, there must be present a photoreceptor (a pigment) cap able of absorbing visible wavelengths of light and then causing the photoinactivation of IAA.

In the action spectrum for oat coleoptile curvature, maximum curvature occurs at about 445 mp. If curvature is caused by the photoinactivation of auxin on the illuminated side of the coleoptile, then the action. spectrum for curvature can indirectly be considered an action spectrum for auxin destruction. If the destruction of IAA by visible light involves a pigment absorbing in the visible region, then the absorption spectrum for that pigment should follow closely the action spectrum for the destruction of IAA. Two pigments have been found in plant cells that have absorption spectra closely resembling that of the action spectrum for cat coleoptile curvature (Figure 17-10). The two pigments are B-carotene and riboflavin. However, the question of which pigment might be involved in the destruction of 1AA is still unanswered.

Evidence supporting riboflavin as the photoreceptor in auxin inactivation has been provided by in vitro systems. Perhaps the most damaging evidence against Bcarotene is that plants containing no Bcarotene will respond positively to a unilateral light (Wallace et al., 1954). In fact, B-carotene has been assigned a protective rather than a destructive role by some investigators. Interfering with light ab sorption and acting

as an alternate substrate for oxidation are two possible ways protection by B-carotaie might be accomplished (Reinert, 1952; 1953).

At the present time the photoinactivation theory has only a small following. One reason for this is that in vive photoinactivation has never been adequately demonstrated. Moreover, there are a disquieting number of studies which have failed to show any real difference in the total quantity of auxin following unilateral illumination.

photoreceptor must be presents that light can provide the energy necessary for lateral transport. For reasons discussed in the previous section, f-carotone and be Havin are the two pigments that have received the most attention in this respect. However, unequivocal proof of the activity of these pigments in phototropism is lacking,

In opposition to the lateral transport theory, there have been numerous studies which have failed to show a lateral distri- bution of labeled auxin when CWIA was exogenously supplied to phototropic ally stimulated coleptiles Binning all 1956; Gordon and Eil, 1956; Riemer, 1958). However, Briggs (1964) la pointed out that in all of these studies the total tissue radioactivity was considered instead of only the amount of radioactivity emerging into collecting agar blocks. Since the phototropic response is due to win in transit, an amount which represents only a small portion of

the total auxin present. an analysis of the total tissue radioactivity could possibly obscure any differential present in auxin being transported.

induced inhibition of basipetal transport of auxin (Gori W ib, 1964; Nagi, 1967; Show.Milly Garden, 1966). Inhibition of basipetal transport on the illuminated side of a milaterally illuminated coleeptile will result in a positive curvature. Excised coleoptile tips from com seedlings which have been illuminated bilaterally have been shown to transport 40% less auxin than coleoptile tips from seedlings which have mot been mad IN 1967). In addition, bilateral illumination of coleoptiles involved in an A W curvature test (auxin csogenously supplied) will cause approximately a 30% reduction in curvature. These findings, coupled with the fact that light-induced lateral transport of xogenously supplied C IAA still needs to be demonstrated provide strong opposition to the lateral transport theory. However, advocates of the theory that hasipetal transport is inhibited by light will need to demonstrate how this inhibition takes place.

Lateral transport of anxin

There is a bare body of evidence supporting the theory that unilateral illumination is a ble of inducing latural transport of nuxin (Brices 1963, 1964; w et al., 1967). That phototropism is controlled by light induced transport of auxin was first hype thesized independently by both Cholodny (1924) and Went (1924). Accordingly.

their explanation became known as the Cheldu r hry. This theory has been revived, extended, and vigorously defended by W. R. Bring and his co workers at Stanford University. Through the use of completely and partially split com coleoptile tips they demonstrated that in diffusing into agar Wocks from

unilaterally illuminated coleoptile tips is much more highly concentrated on the shaded siden 1967; 1964: et al., 1963). Moreover, there is no appreciable loss of aukin from illuminated is compared to dark controls, a finding that contradicts the photoinactivation the ory (Figure 17-11).

Note in Figure 17-11 that when the coleoptile tip is only partially split with a thin glass barrier-leaving the extreme tip intact-the shaded side contains almost twice as much auxin as the illuminated side However, when the tip is completely divided there is no longer an unequal distribution of auxin.As in the photoactivation theory, Inhibition of basipetal transport of in Recently there have been a number of studies which support the idea that the phototropic response is caused by a light

Geotropism

an intact seedling is placed in a horizontal position it will respond to the carth's gravitational field with a particular pattern of growth. Growth of the stem under these

for root cell clongation. The combined effect of retardation of well elongation of the lower side and slightly stimulated cell elongation of the upper side results in the root curving downward.

An explanation of how gravitational pull influences lateral transport of autin l l clades us. The simplest explanation would be that it is the natural reaction of a substance which contains mass to gravitational pull. However, there are several studies which t that cotropically induced lateral movement represents an active transport of auxin (Harrison, 1965; will al., 1967). If this is true, we should not be able to detect a gootropic response by plants under anaerobic con ditions. A lack of peotropic response under anacrobic conditions has been shown by some stadies (Harris, 1965; Wilkinson 1967) but not by others (Nagri al., 1965). Also some investigators believe that stato liths, which move under the influence of g ravity, we reponsible for the lateral movement of auxin in grotropism (L . 19: 1965). How the movement of stato liths under the influence of gravity stimubates lateral transport ol in is not yet clear

of many plant species reflect the influence of apical dominance Plants that grow tall and unbranched reflect a strong influence while plants that are short and shrubby give evidence of a weak influence of apical dominance.

The strong influence of the apical bud on the growth of lateral buds is easily demonstrated by removing it from the plant in the absence of the apical bud. active growth begins in the lateral bud However, in a short time the lateral bud nearest the apical bud will establich dom inance over the remaining buds, causing them to become inactive rain

The first lint that apel dominance

might be because of auxin produced at the terminal bed and transported downward through the stem was given in Mudies by Skoog and Thimann (1937). Removal of the terminal bud of the broad bean and its replacement with a block of agar resulted, Almight be expected, in lateral bud growth Replacement of the terminal bud with

ear blocks containing IAA, however, suppressed lotsal bud growth in much the a me manner as the terminal bud (Figure 17-12)

Previous to the experiments of skoop and Thimann, it had been noted that the apical bud contained a much higher auxin content than the lateral buds. This fact

-

in

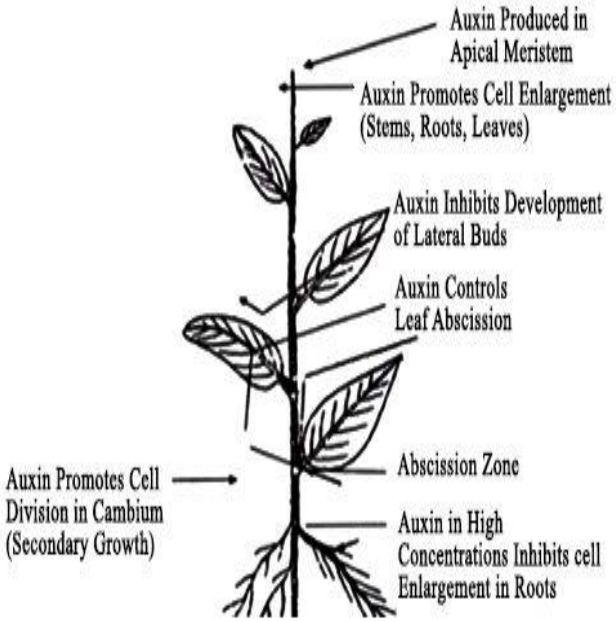
circumstances will cause it to curve up ward until it is vertical again and the root system will curve downward until it to is vertical again. Accordingly, we refer to the stem as an organ which exhibits maie greps and to the root as an organ which exhibits

w ana Like phototropium, the corp ree is controlled by an equal distribution of auxin but, unlike phototropism, tramite inal pull instead of light is the influencing factor in geotropic auxin distribution

The Cholodny-Went theory provides an explanation for gootropism as well as platotropism. They peoposed that the differential growth exhibited by a hori zontally placed organ is due to the accumu- Intion of aukin on the lower side. They suggested that suinis laterally transported from the upper to the lower side under the influence of gravity. This was quite clearly shown as early as 1930 in the work of Doll (19.) with cat and com coletile tips He noted that the oritation of the op had no effect on the totalment diffusing out of the time. However, much cater amount of in diffed out from de lower half of the hormonally placed cole optile tip than from the upper half. Dolk's ex criments have been teated by several investigators (Gillespidol 1 : 193; Golemikal. 1967 with similar results.

The accumulation of aukin on the lower side of a horizontally placed stem causes an accelerated growth tou r on the lower side causing the stem to curve upward. The horizontally placed Toot, however, will exhibit a witive geotropic response even

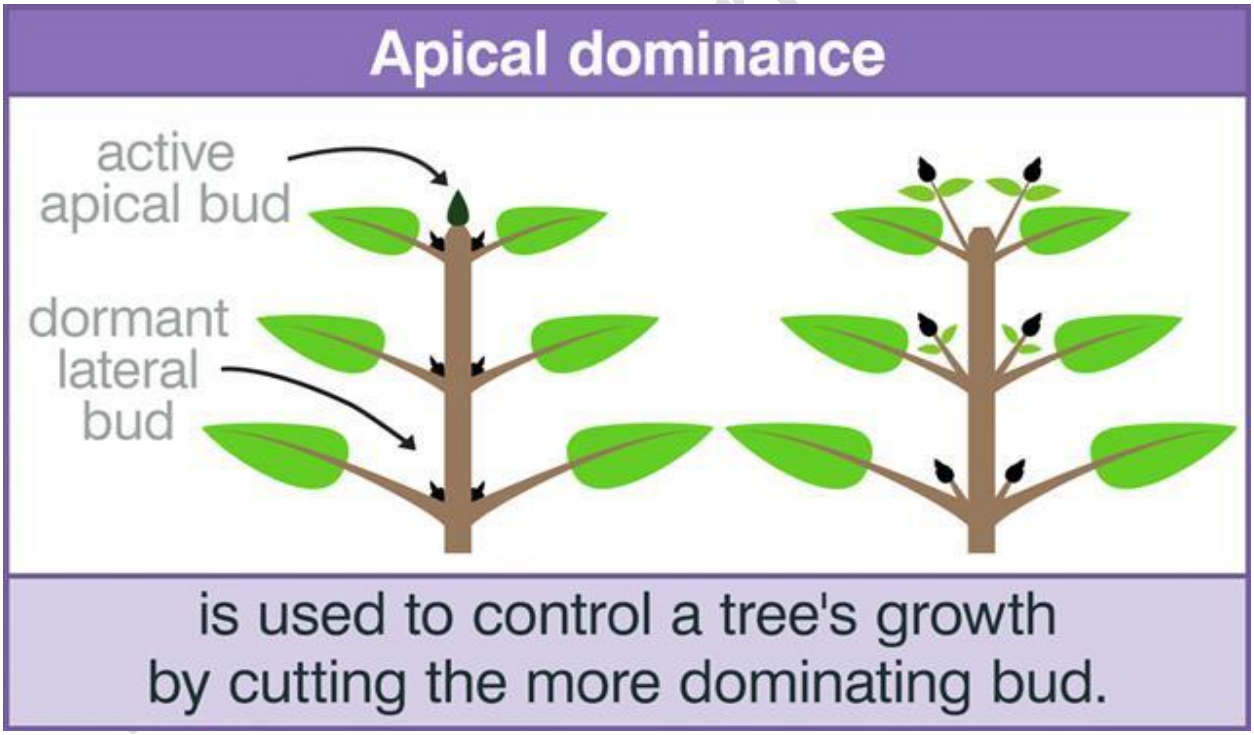
though in concentrate on the lower side, Roots are much more sensitive to IAA than stoms and the concentrations of IAA which wimulatu cell elongation in Ses are actually inhibitory collelongs tionin re . The accumulation of on the lower side of a horizontally placed root would therefore, retard cell elongation on that side. We should also consider that the concentration of IAA in the upper side may be reduced to the simulatory level.



Apical dominance

Long before the discovery of hormonal regulation in plant growth, the peculiar dominance of apical over lateral growth soon in eat many species of plants had been noted by bonists. They had observed that the apical or terminal bud of many Vascular plants was very active in growth while the lateral beds remained inactive. the same

phenomenon was observed in the new Joot growth of many tree species In fact, the characteristic growth pats. They investigated the nutritional aspects ofapical dominance with sucne repuls, It was found that the influence of in on lateral bed growth is controlled by the nutritional status of the plant. If the nitrogen needs of a flax plant are completely supplied during its growth, then, at the optimal period of growth, lateral bad inhibition by applied in cannot be demonstrated. However, in fax plants grown undcrcondition of inadequate nitungen supply, the influence of applied auxin on Lateral bed growth is easily demonstrated.



root clongation, but com a noticeable increase in the number of branch root. Application of IAA lanolin paste to the severed end of a young wom stimulates the

rate of formation and number of roots initiated. This discovery is not only of scientific interest, but also has opened the door to commercial application of IAA to promote root formation in cuties of economically useful plants. Figure 17-14 illustrates the effect of IAA and two SDthetic auxins on root formation in bean seedlings undoubtedly led to the experiments with The apical bod is not the only source of the broad bean. However, physiologists to auxin. Young developing leaves also prothis day have been unable to explain why duce auxin, and it has been shown that lateral bud growth should be inhibited by auxin from this source may inhibit lateral a much smaller amount of auxin than isbud growth (Roveller w Jacobs, 1955). found in the apical bud, wlaich, to make the Presendy, the above explanation of apical problem more complex, grows vigorously bud dominance has been receiving an inin the presence of this relatively high con c reasing amount of criticism from a nucentration of auxin.

ber of different investigators. For example, Although the problem of apical domin-studies done on the lilac (Syring Hilaris) ance did not lend itself to casy solution, it have demonstrated that the auxi-poor did cause a great deal of speculation in the mature leaves of this plant have a much botanical world. Many theories were pre greater influence on tal bed inhibition posed with varying degrees of acceptance than the auxin-rich terminal bud (Clamp until Thimann, in 1937, suggested that war,

1955). In addition, latcral bindini lateral buds respond to auxin in much the bition not only occurs below the mature

me mar a tots and shoots, that is caves on the stem, but above them also to minimum, optimum, and maximum Because of the upward movement of the concentrations. Concentrations of auxin auxin influence on the stem, Champagnat above that which will give the maximum (1955) has claimed that auxin may not be Concentration will cause inhibition (gure involved in apical dominance. But, as we 17-13). Thimann claimed that lateral buds discussed carlic, nonpolar movement of are more sensitive than ens to in and SUNID has been demonstrated in several that the concentration of auxin that stimu- cases, making it very possible for an influ lates stem growth is inhibitory to lateral ence of anxin to be felt in an upward direcbud growth. This theory received general tion from its origin as well as in a downacceptance, although it still failed to explain wand direction. why the apical bud should be less sensitive The most provocative criticism of Thi to auxin merely because of its location on mann's theory on apical dominance has the stem.

been given by Gregory and Veale (1957).

ParthPY With pollination and the subsequent fortiliatinn of the ovule of a flower, the complex growth pattern leading to fruit set begin. Growth of the ovary wall and

in some cases the tibes associated with the tereptacle is greatly accelerated. Most of chis acceleration of growth is due to cell.

Root initiation

As already discussed, removal of the tip of adoo greatly reduces the shoot's growth rate. In contrast, the removal of the tip of a root does not appreciably affect the growth rate (Hot and Th , 1937). In fact, removal of less than 1 mm of the tip results in a very small but significant stimulation of growth rate (Chelodiny 1926). Replacement of the trip will again retard root growth (Cholery, 1926 and 1931). Coleoptile tips have been found to act in the same manter as the root tip, Tetarding root growth when substituted for a rootti Tlucre is little coube chat both the root tip and the coleoptile tip secrete substance inhibitory to root growth. This substance has been identified as IAA (Rapla al 1934

The questionaries, is the action of auxin fundamentally different in roots as compared to stoms?. It has, more recently, been found that the action of auxin in roots is similar to that in stems, but that the con centrations of aux simulatory to stem growth are inhibitory to root growth. In other words, roots are much more sensitive to auxin than stems (Figure 17-13). and real stimulation of root donation may be achieved if low concentrations a resed (Delid Jackson, 1961; cum 1960)

The application of relatively high on concentrations of IAA retards.

It appears from the above description of fruit set that pollination and fertilization are in some way connected with development of the fruit-perhaps with the release of a stimulus of some kind. Fruit development in the absence of pollination does, however, occur and in fact is relatively common in the plant world. The development of fruit in this manner is called parthenocarpic developinent, and the fruit that is formed is called parthenocarpic fruit.

The fact still remains that in the great majority of cases fruit development does not occur if fertilization does not take place. In what manner, then, does fertilization of the ovule trigger off responses leading to fruit set? As far back as 1902. Masurt had demonstrated that swelling of the ovary wall of orchids could be stimulated by dead pollen grains. "Following Massart's work, Fitting (1909) observed that water extracts of pollen are capable of inhibiting floral abscission and stimulating ovary wall swelling in orchids. Due to either a lack of interest or the complexity of the investigation, the problem of parthenocarpic fruit development lay dormant at this level for over 20 years. In 1934, the problem was again opened by Yasuda (1934), who succeeded in causing the development of parthenocarpic fruit with the application of pollen extracts to cucumber Bowers. An analysis of the materials present in such extracts showed that auxins were present (Thiman, 1934). Finally,

Gustafson (1936) demonstrated that parthenocarpic development of fruit could be induced by application of 1AA in lanolin paste to the stigma of the flower.

It was later found (Muir, 1942) that immediately after pollination, there is a sharp rise in the auxin content of tobacco ovaries. In the absence of pollination, no increase in auxin content is observed (Figure 17-15). Muir (1947) also observed that growth of the pollen tube increases considerably the amount of extractable auxin

Auxin content, degree curvature

in the style of tobacco plants, leading him to suggest that an enzyme may be released by the pollen tubes which catalyzes the production of auxin. This suggestion was later given support by Lund (1956) who found that pollen tubes secrete an enzyme capable of converting tryptophan to auxin. It is obvious from the above discussion that auxins play an important role in the development of fruit. It appears that pollination, growth of the pollen tube, and ferti lization all contribute to the "gush" of auxin responsible for fruit development. Although significant, the amount of auxin found in pollen grains is not sufficient to account for the high concentration of auxin found in the ovary after fertilization (Gorter, 1961). However, as we have already suggested, an enzyme may be released by the growth of the pollen tube which is involved in the synthesis of auxin, perhaps from a precursor such as tryptophan.

Natural parthenocarpic fruit development is quite common in the plant world, leading some to suggest that auxins arenot involved after all in the development of fruit. However, Gustafson (1939) found that in the ovaries of species capable of natural parthenocarpy, the auxin content is a great deal higher than that found in the ovaries of species needing fertilization to produce fruit.

Abscission

The controlling influence of natural auxins on the abscission of leaves was first suspected when Laibach (1933) showed that a substance contained in the extract of orchid pollinia is capable of preventing abscission. Support of this observation was given by LaRue (1936) when he demonstrated the delaying effects of various synthetic auxins on the abscission of Coleus leaves. Since that time, a great deal of confirmatory work has been performed, clearly estab lishing indole-3-acetic acid (IAA) as the primary controlling factor in the abscission of plant organs (Addicott and Lynch, 1955). Before the abscission of a plant organ, a layer of tissue is usually formed at the base of the organ, this tissue being easily distinguished from the surrounding tissues. This layer of tissue is referred to as the abscission zone. Cells in the abscission zone appear to be thin-walled and are almost completely lacking in lignin and suberin (Scott et al., 1948). In most cases, a series of cell divisions precede separation, although separation in the absence of cell division has been found in

several species (Addicott and Lynch, 1955). The indication is that cell division is not essential to separation, but important in the forming of scar tissue, which acts as a protective layer over the wound left by abscission (Gawad and Avery, 1950).

to the abscission of a plant organ? It is a well-known fact that removal of a leaf blade will cause, in a short period of time, the abscission of the petiole. As discussed before, one of the sites of auxin production is the leaf blade from which auxin is transported through the petiole into the stem. Auxin, therefore, has been suspected as a controlling factor in abscission. This was clearly illustrated by Shoji et al. (1951). They found that auxin content is high in the immature bean leaf bade, compared to the petiole, but that as the leaf ages, the auxin content of the blade falls to a point comparable to that found in the petiole (Figure 17-16). At this point, the leaves are yellow and ready to abscise.

In a simple but ingenious series of experi ments, Addicott and Lynch (1951) demonstrated that the most important factor controlling abscission is the condition of the auxin gradient across the abscission zone. Application of IAA in lanolin paste to either the proximal or distal (away from the stem) end of debladed bean leaf petioles has a profound effect on the rate of abscis sion of those petioles. Proximal application accelerates the rate of abscission and distal

In a review on the subject of abscission, Addicott and Lynch (1955) have listed three types of dissolution phenomenon that may cause abscission. In some cases, the middle lamella dissolves between two layers of cells, the primary walls remaining intact. The middle lamella and the primary wall may both dissolve, and in a few examples, whole cells have dissolved. Botanists have sought to answer the question, what are the factors leading up

application retards it (Figure 17-17). It was concluded that a critical auxin concentration gradient across the abscission zone, rather than the concentration itsdlf, may be necessary to prevent abscission. According to this theory, abscission does not occur when the gradient is steep, that is, when the endogenous auxin concentration is high on the distal side and low on the proximal side of the abscission zone. Abscission occurs when the gradient becomes slight or neutral and is accelerated when the gradient is reversed. These relationships are shown diagrammatically in Figure 17-18. It is interesting to note that Rossetter and Jacobs (1953) found that the intact leaves of Coleus speed abscission of nearby debladed petioles, suggesting that the intact leaves act as sources of proxima! auxin for nearby petioles. Also in bean, application of IAA to the distal tip of one of a pair of opposite debladed petioles accelerates the abscission of the untreated petiole (Devlin, 1964; Devlin and Hayat, 1966).

Respiration

James Bonner (1933) was the first investigator to recognize that auxin has a stimu

Distal

region

Endogenous auxin

Abscission zone

Proximal region

Distal region

No Abscission

latory effect on respiration. His work led him to suggest that auxin activity only takes place in the presence of oxidative metabolism. Since Bonner's pioneer work many studies have confirmed that auxin stimu lates respiration and that there is a correla tion between increased growth due to auxin treatment and increase in respiration. In Figure 17-19, a striking similarity can be seen between the response of growth

Abscission zone

100

Percent abscission

ao

60

Abscission

40

20

Proximal region

Ausin on proximal end

Time after treatment, days

17-17 Effect of proximal and distal applications of auxin (105 mg/er) on the rate of abscission of dehladed bean leaf potioles. (After F. T. Addicott and R. S. Lynch. 1951. Science 114: 688)

Exogenous ausin

Control

Distal region

Auxin on distal end

Proximal ragion

Accelerated Abscission

Relations between the auxin gradient aerous the abscission zone and abiciusion. (After F.T. Addict and R. S. Lynch. 1955. Ann. Rev. Plant Physiol. 6: 211.)

Respiration as percent of control

Respiration

Concentration of auxin influence of IAA on the synthesis of new RNA and protein. Both synthetic reactions require an expenditure of energy and as such would cause an increase in respiration. Also in all probability, the activity of enzymes synthesized as a result of IAA stimulation would bring about an increase in respiration.

The effect of different concentratices of amain on the rate of growth and respiration of corn coleptile sections. (After R. C. French and H. Beovers. 1953. Am. J. Botany 40: 660.) and the response of respiration to different concentrations of IAA. The optimal response for both curves occurs at almost the same concentration of IAA.

Physiologists are still faced with the problem of explaining how auxin induces a stimulation of respiration. An attractive approach to the problem has been made by French and Beevers (1953). They dem onstrated that respiration may be increased by substances that have no effect or an inhibitory effect on growth. Dinitrophenol (DNP), a substance which inhibits oxidative phosphorylation (formation of ATP from ADP in respiration), increases the rate of respiration while inhibiting growth. Since the rate of respiration is normally limited by the supply of ADP, treatment of living tissues with DNP should cause an increased supply of ADP and thus stimulate respiration. It is thought that auxin may also increase the supply of ADP by causing ATP to be rapidly used up in the expanding cell, thus increasing the supply of ADP. This would appear to give auxin an indirect role in the stimulation of respiration rather than the direct role that was earlier postulated. We have already discussed the stimula

Callus formation

Although we have been stressing that auxin activity manifests itself in the plant primarily as a stimulant of cell elongation, it also is active in cell division. For example, application of 1% IAA in lanolin paste to a debladed petiole of a bean plant will cause a yellow swelling where the auxin is applied. This swelling is caused by the development of callus tissue made up of rapidly dividing parenchyma cells. If a

succulent stem is cut a few millimeters below a mature leaf and the wound treated with 1AA in lanolin paste, this same proliferation of parenchyma cells is observed. After a period of time, young adventitious roots will develop. Thus, IAA not only causes a proliferation of cells, but also under some conditions may cause à dedifferentiation of these cells, that is, cause the formation of adventitious roots.

Also, in many tissue cultures where callus growth is quite normal, the addition of auxin is necessary for the continued growth of such callus. The amount of callus tissue formed is related to the concentration of IAA applied, higher concentrations causing greater development of the callus tissue. (Figure 17-20).

Bioassays

When dealing with biologically active. substances, such as plant growth hormones, it is essential that a means for measuring their activity be obtained. In most cases, the material used to measure the activity of a growth regulator responds specifically tofrom tryptophan

test is even more sensitive than the Arme curvature test, being able to detect con centrations of IAA as low as 1/10).XImg However, snall differences in auxin con- centration cannot be detected by the root test, its response being roughly proportional to the logarithm of the auxin con- centration

extraction procedures was a source of error in early work with IAA It was soon discovered that boiling the plant material (Gustafss, 1941) or extracting at low temperatures Wild Aur 1949) effectively limited the synthesis of LAA The above discoveries gave support to the suggestion by Skoog and Thimann (1940) that the production of auxin is an enzymatic process. Finally, an enzymatic system capable of converting tryptophan to IAA was isolated by Wildman et al. (1947) from spinach leaves.

Detailed stadies on the presence of an enzyme capable of converting tryptophan to IAA in Avena coleoptiles have demonstrated a close agreement between the distribution RIAA and the enzyme (Wild

and B T, 1948). The enzyme is present in greatest amount at the tip and is progressively less concentrated toward the base of the coleoptile.

The biosynthetic pathways by which tryptophan might be converted to TAA are illustrated schematically in Figure 1725. Gordon and Nicva (1949) found that if

Biosynthesis of Auxin

In the carlier years of auxin study, Bonncr (1932) found that the mould increased its output of natural amin if grown in a medium containing peptone. R um, at that time, was one of the best sources of natural auxin. This increase in a supply undoubtedly

Cred through the oxidation of the amino acids of peptone. Three years later, it was demon- strated that this mould could convert the amino acid tryptophan to IAA (human, 1935). To this day, tryptophanis con- sidered to be the primary precursor of

leaf discs or crude extracts of pineapple leaves are incubated with tryptoplan, tryptamine, or indolepyruvic acid, AA formed. They proposed that IAA could be formed from tryptophan via two different pathways: by the deamination of trypto plan to form indolepyruvic acid, followed by decarboxylation to form indoleacet- aldehyde or by the decarboxylation of the tryptophan to form tryptamine, followed by deamination to form indolatalde hyde. By cather pathway. indoleacetalde hyde is formed and thus must be considered the immediate precursor of IAA in plants. One or both pathways have been detected in a variety of plant material

and Mir, 1967, Mona S , 1957; Phelys Gud Segueira, 1967), Indolcacetaldehyde is readily oxidized to form LAA. Its conversion to the win has been demonstrated on several occasions, ung crude enzyme preparations from different plants (Shoe ol, 7951),

Gordon (1961) in a review on the subject of in biosynthesis, suggested that ausin may be formed by different pathways during the development of the plant. In other words, the biochemistry of auxin formation in germinating seeds may be different from auxin formation in leave coleoptile tips, etc. He draws a parallel in this respect

to the glycolytic pathway. There are many examples where clucose oxidation follows different pathways dur mg the ontogeny of the plant.

Other Plant Hormones Ali II in 1945 a group of scientists at the University of California (Davis) isolated a naturally occurring inhibitor from cotton fruit which they called as Ollo , 1965) The molecular structure of abscisan 11 is given below.

THE GIBBERELLINS AND CYTOKININS

Gibberellins If it were not for the balanse discate, which had devastating effects on the rice conomy of Japan, the existence of gibberellins in plants might still be unknown. Japanese farmers noted that plants affected with this disease were taller, thinner, and paler than their normal counterparts and sometimes were devoid of fruit (Phimmey and West, 1961). Crop losses as high as 40% were reported. Noodless to say, the Japanese scientists were interested in the cause of the disease and its control

In the carly part of the twentieth century, an extensive program of research into the cause of bakane disease was initiated. Japanese pathologists first demonstrated che connection between the balanae disease and the fungus called Furmanowilifonu Sheld Girella fami(Saw.) Wr.). It was then postulated by Sawada (1912) that the disease may be caused by something secreted by the fangus. This postulstion was given experimental support by Kurosawa (1926), who demonstrated that sterile

filtrates of the fungus are capable of causing the symptoms of bakanac discase in otherwise normal rice seedlings. Finally, in 1938, Yabuta and Sumiki were able to isolate the crystalline gibberellin. Since that time, gibberellins and gibberellin-like substances have been found in higher plants (Mitchell et al., 1951; Simild and Keda, 1961; l'estand Phucy, 1957).

Chemistry of the gibberellins Several compounds lave now been isolated with biological activity similar to that of the original gibberellin isolated from the fungus G. fujikurei. So far, thirteen natu- rally occurring gibberellons have been found, all having very similar chemical structures (Palce. 1965). The chemical structures of these compounds, sometimes referred to as the gibberellin A series, are given in Figure 19-1. All of these compounds poses the same general carbon skeleton and all are able to promote either stem elongation or cell division or both in plants. However, their relative effective ness in these promotions are quite often quite different (Figure 19-2).

flowering plants to exogenously applied gibberellins, they should be regarded as natural plant growth hormones. Indeed, they have been compared to IAA in their biological activity, although in some cases they act in a different manner (Table 19.1) and in other cases in a similar manner Gul d Purpes, 1960). Gibberellins act Similarly

to IAA in that they promote cell clongation induce parthenocarpy, and induce new RNA and protein synthesis

We will cover in the following discussion the influence of gibberellins on genetic dwarfism, bolting and flowering lightinhibited plants, parthenocarpy, and mobilization of storage carbohydrates during germination.

Physiological effects Because of the widespread distribution of gibberellins in plants and because of the different specific responses of individual

Genetic dwarfism

One of the most striking properties of the gibberellins is their ability to overcome genetic dwarfism in certain plants. Usually in such cases, dwarfism is caused by the mutation of a single gene. Photooxidation

It has long been known that IAA can be inactivated by ionizing radiation. Skoog (1934; 1935) demonstrated that rapid inactivation of pure IAA takes place when it is subjected to x- and gamma-radiation. He also noted that little, if any, inactivation takes place in a nitrogen atmosphere, sug gesting that inactivation is due to oxidation by peroxides formed during irradiation (Galston and Hillman, 1961). There is some evidence that only a small amount of IAA is inactivated or oxidized in this manner, most of the detrimental effect of this type of irradiation to IAA being of an indirect

nature. For example, Gordon (1956) has claimed that the major effect of ionizing radiation on auxin metabolism may be

found in the destructive effect of the radia tion on the enzyme system converting tryptophan to IAA.

Ultraviolet light also inactivates JAA. This might have been predicted because of the ring structure of the IAA molecule, which absorbs to some extent in ultraviolet (maximum absorption at about 280 m). Here, there is a direct effect on the IAA molecule due to the absorption of ultraviolet light. Determinations of auxin content before and after irradiation with ultraviolet light have shown that this type of irradiation reduces auxin levels in plants (Burkholder and Joeluston, 1937; Popp and Mellraine, 1937).

CYTOKININS

If it were not for the balanse discate, which had devastating effects on the rice conomy of Japan, the existence of gibberellins in plants might still be unknown. Japanese farmers noted that plants affected with this disease were taller, thinner, and paler than their normal counterparts and sometimes were devoid of fruit (Phimmey

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Bolting and flowering

In addition to their role in internode elongation, gibberellins function in many plants as a controlling factor in a balance between internode growth and leaf development. For example, in many plants leaf development will be profuse, while internode growth will be retarded, a form of growth called a "rosette." Just before the

reproductive stage, there is a striking stimulation of internode elongation, the stem sometimes elongating from five to six times the original height of the plant.

Usually this type of plant is a rosetted "long-day" plant, requiring a certain minimum number of hours of daylight to bolt and flower or a rosetted "coldrequiring" plant, needing a cold treatment to bolt and flower. If the long-day plant is kept under short-day conditions and the cold-requiring plant is not given a cold treatment, the rosette form of growth is maintained.

concentration or presence, may ultimately lead to the differentiation of floral pri mordia. In addition, gibberellin treatment of short-day plants under photoperiods unsuitable for flowering does not promote flowering (Sirenval, 1961). In fact, in at least one case, gibberellin treatment of short-day plants under conditions favorable to flowering actually reduced flowering (Harder and Binsour, 1956).

It appears that the reason a plant either remains in the rosette form or bolts and flowers is related to the amount of native gibberellin present in the plant. For example, there is some evidence that native gibberellin-like substances are found in greater amounts in the bolted plant than in the nonbolted form. In addition, higher concentrations of gibberellin-like substances have been found in the bolted coldrequiring plant Chrysanthemum morifolium Ram. ev. Shuokan and in the long-

day plant Rudbeckia speciosa Wenderoth than in the nonbolted forms (Harada and Nitsch, 1959; Nitsch, 1959).

Treatment of these plants with gibberellin during conditions that would normally maintain the rosette form will cause the plant to bolt and flower (Lang, 1957; Lang and Reinhard, 1961; Stuart and Cathey, 1961). It is even possible to separate bolting from flowering by controlling the amount of gibberellin applied; that is, a plant will bolt but not flower if a smaller dosage of gibberellin is applied (Phinney and West, 1961).

The separation of bolting and flowering in gibberellin treatment of rosetted plants has led some investigators to suggest that flowering is only an indirect result of gibberellin treatment. The stimulated elongation of the stem necessitates the produc tion of the many compounds needed to maintain such intermodal growth. Some of these compounds, by either their con

Light inhibited stem growth Anyone comparing the stem growth of an etiolated plant (dark-grown) with that of a lightgrown plant will immediately conclude that light has an inhibitory effect on stem clongation. Application of gibberellins to certain plants growing in the light will greatly increase their stem growth. With the above facts in mind, we are presented with the question, is there a relationship or interaction between endogenous gibberellin and light absorbed by the plant?

The reversal of light-induced inhibition of stem elongation by application of gibberellin suggests that endogenous gibberellin is the limiting factor in stem growth, The most obvious conclusion is that light causes inhibition of stem growth by lowering the level of available gibberellin in the plant. This inhibition is overcome by applying exogenous gibberellin to the plant. However, investigation along this line of reasoning has put this very simple solution in doubt.

Lockhart (1961), a proponent of the theory that light lowers the level of available gibberellin in the plant, has shown that increase in the level of available gibberellin increases the plasticity of young cell walls. In previous discussions, we have mentioned the importance of cell wall plasticity in cell elongation. Lockhart has also demonstrated that plasticity of the cell wall is decreased in the light-grown cells (Figure 19-4). He concludes that exposure to light lowers the level of endogenous gibberellin, which in turn decreases the plasticity of the cell walls, thus inhibiting stem growth. Application of exogenous gibberellin counteracts light-induced decrease in plasticity (Figure 19-4). Evidence that red light irradiation retards the conversion of a gibberellin precursor to gibberellin has been found in a study of stem elongation in bean (Phaseolus vulgaris ev. Pinto) (Lorb hart, 1964). Obviously, this results in a red light inhibition of stem elongation that can be overcome by exogenously applied

356

Bonding, degrees

10

50

00

Treated with bbc acid

Irradiated

Dark grow

GA. Thus, in this plant at least, we have evidence of a light mediated decrease in the level of gibberellin in the plant.

In the work of Mohr and Appuhn (1961) and Mohr (1962), an argument may be found against the theory that light inhibition of stem elongation is caused by lightinduced lowering of the gibberellin level in plants. Stem elongation of mustard seedlings grown in the dark may also be stimulated by application of gibberellin. in fact, the concentration of gibberellin needed for maximum response is the same for both dark- and light-grown mustard seedlings. This could not be so if light lowered

the endogenous level of available gibberellin in the plant. There is always the possibility that light stimulates the production of inhibitors which interfere with the activity of GA in stem elongation. Evidence supporting this possibility has been found in studies of GA activity in pea stem elongation (Kende and Lang, 1964; Kohler and Lang, 1963).

Whether gibberellin-induced elongation and light-induced inhibition of stem

4 B 12 26 200 Minutes

Untreated

4

Irradiated

Dark grown

12 10 20

19-4 Plasticity of the cell wall of elongating cell in dark-grown and irradiated Alaska pea stems. The irradiation treatment consisted of a 3 hour exposure to red light. Gibberellic acid was applied 3 hours prior to irradiation. Plasticity is here measured as the amount of residual bending after a weight is removed. Note dat plasticity was

not decreased by irradiation when gibberellic acid was applied. (Reproduced from Ma Crash Regulation, edited by R. M. Klein, 1961 by Jowa Suse University Press.)"

growth act independently of each other is still as yet unsolved. Certainly, there seems to be arguments for both conclusions.

Parthenocarpy

In a previous discussion, we described how application of auxins could cause fruit to develop parthenocarpically. In the early years of this discovery, it was thought that auxin activity after fertilization was the primary mech anism of fruit development. In fact, substitution of exogenous auxin for fertilization became a highly valuable venture into the economics of fruit growing.

However, auxins are not the only natural growth hormones capable of inducing parthenocarpy. Gibberellins have been found very reliable in producing parthenocarpic fruit-set and, in many cases, show higher activity than the native auxin in this respect. In fact, there are several examples where auxiu has proven ineffective and gibberellins active (Devlin and Demoranville, 1967). For example, pome and stone fruit have been generally unresponsive to auxin treatment (Winter and Bukovar, 1962). Yet, gibberellins have induced parthenocarpy in both pome (Davison, 1950; Lucill, 1959) and stone Crane et al., 1960; Rebelz and Crane, 1961)

fruits. There is little doubt that native gibberellins and gibberellin-like substances play a major role in the development of fruit under natural conditions. Whether this is a direct action by gibberellins or an interaction with the native auxin' of the plant has not been conclusively shown. A comparison between gibberellin-induced parthenocarpic fruit and fruit developed normally after fertilization is given in Figure 19-5.

Mobilization of storage compounds during germination A longitudinal section through a mature cereal grain will reveal that its greater bulk is composed of two major parts, the embryo and the endosperm. The endosperm consists of a mass of dead starch-laden cells surrounded by a layer

Inducement of parenthocarpy in Wealthy apple fruits with gibberellins A, and A. (Repro duced from Plaw Gorth Regulaties, edited by R. M. Klein, 1961 by Jowa State University Press.)

of living cells called the aleurone. The embryo, of course, represents the future adult plant. Growth of the embryo during germination depends upon the mobiliza tion of stored starch in the endosperm. By mobilization we mean the enzymatic breakdown of the stored starch to simple sugars and the translocation of these sugars to the embryo where they will provide an energy source for growth. Up until 1958 it was thought that the endosperm played only a passive role in germination that the embryo

provided the enzymes for the breakdown and mobi lization of the endosperm starch reserves. However, Yomo, a Japanese scientist, demonstrated that under aerobic conditions barley endosperm, separated from the embryo but incubated with it in the same culture flask, could exhibit amylase activity (1958). No amylase activity was observed in culture flasks containing either the em bryo or the endosperm alone. From his experiments Yomo concluded that amylase activity in the endosperm is controlled by an unknown factor produced in the embryo. Yomo (1960; 1960) and Paleg (1960; 1960), working independently, concluded that the unknown factor was gibberellin. Both investigators demonstrated that exogenously applied gibberellic acid (GA) could stimulate amylase activity in isolated barley endosperm. Even more significant, Paleg (1960, 1965) was able to show that the enzymes a-and B-ainylase and possibly.

PHOTOPERIODISM

Undoubtedly, even before the dawn of history. man was at least subconsciously aware of the controlling effect of light on plant growth. One can imagine that it was easily demonstrated cat a plant could not grow in the dark, chat light was essential. Surprisingly enough, however, this was not even suggested until 1779 when Ingenhouse recognized the importance of light in photosynthesis. Since that time,

there has been slow but steady progress toward the recognition of many light-controlled processes involved in plant growth.

Prerequisite to the initiation of a plant response to light in the requirement that light be absorbed. This means a receptor of some sort (usually a pigment) has to be present and be capable of absorbing the wavelength or wavelengths of light responsible for the response. In many cases the absorbance of light by the receptor Causes it to become more reactive, which in turn starts sence of chemical reactions, leading ultimately to a peneral plant res . The absorbence of light with subsequent activation of the absorbine molecule, followed by a series of chemical reactions leading to a general plant response, may be formed a plan helelal process.

Many of the photobiological processes occurring in plants have been studied extensively by scientists, and in veral cases individual con s of these pro cesses have been isolated and caracterized. Some of the photobiological processes.

Terminology The Maryland Mammoth mutant was called a short-day plant because of its habit of flowering only under short-day con ditions. It was soon discovered that plants vary considerably in their response to day length. In some plants long-day photoperiods induce flowering, while others appeared unresponsive, flowering under both long and short-day conditions. Still others respond to photoperiods

situated somewhere between short and long-day lengths. The definitions given below are based on a 24-hour cycle of light and dark

that have been studied in detail are ple synthesis, chloroplull sytless, phone ,

dation, and photos. Phot synthesis, chlorophyll synthesis, photo tropism, and photooxidation have all been discussed in previous chapters. We will devote our discussions in this chapter to photoperiodism.

Photoperiodism is a term that escapes precise definition, Generally, it is defined as the response of a plant to the relative lengths of light and dark periods. However, this definition can be modified in many ways. For example, the duration of the dark period is much more important than the duration of the light period. Intensity and quality of light can be modifying features in the magnitude of the response. The total quantity of light received can have an influencing elect. It is generally accepted, however, that the duration and order of sequence is most important in the initiation of a photoperiodic response. Any response, then, by a plant to the duration and order of sequence of light and dark periods may be called a ph r iodic

Plants respond to alteration of light and dack periods in a variety of ways. Flower ing, vegetative growth, interiode clonga tion, seed germination, and leaf abscission are some examples of photoperiodic res ponses that have been discovered in plants.

Since flowering was the first photoperiodic response to be discovered and the one most extensively studied. Our discussion of photoperiodism will largely be an analysis of this phenomenon.

vigorously when planted early in the spring, but remains in a vegetative state if planted in late spring of summer Tournois showed that if hemp is provided with short photoperiods (6 hours), it will flower, but if provided with a long photoperiod, it will remain in a vegetative state.

A study of the flowering habits of Sep by Klebs (1913) showed that powering can be induced by artificial illumination in mid winter in a greenhouse, although the normal time of flowering for this plant is fune, Klebs concluded that flowering in Sewer is controlled by the length of the photoperiod and that light serves as a catalytic factor in this respect.

The first clearly stated hypothesis on photoperiodism was given by Garner and Allard (1920). For an experimental plant, they used a large-leaf mutant of the tobacco plant, which is noted for its vigorous vegetative growth and a flowering habit that differs radically from the normal tobacco plants. The mutant, Maryland Mammoth, does not power in the field, but when brought into the greenhouse, it flowered profusely in mid-December. The following year the seeds from chis plant were sown with the normal type and the pattern was repeated, the mutant remaining

vegetative in the field, but when brought in the greenhouse, Howering again in December

The next step was to subject the Maryland Mammoth tobacco plant to short day lengths during the summer by placing the plant in darkness after exposure to a day length that would be equivalent to a winter day. The mutant then was capable of flowering in the summer. In addition, it was found that the mutant can be kept in

vegetative state during the winter months by merely lengthening the days with Artificial light. It is quite obvious that Maryland Mammoth only flowers under short day length conditions. Garner and Allard termed the response of Maryland Mammoth to day length photoperiodisn.

flower, will not flower if kept under con tinuous short or long plotoperiods.

It is important to note that the above classification is based on whether or not a plant will flower when it is subjected to a photoperiod that exceeds or is less than a critical length. The classification docs not mcan to imply that all short-day plants flower under photoperiods that are shorter than photoperiods inducing flowering in long day plants. An example to amplify this point would be to compare the shortday plant X him with the long day plans H ur . Xant has a critical day length of 15 hours and flowers if this critical value is not exceeded. Hyoscy has a critical day length of 11

hours and will flower when this critical value is exceeded. The significant point here is that Xanti , a short-day plant, and Hyoscyans, a longday plant, will both flower if subiected to a photoperiod of 13 hours. The delimiting factor, then, is not the number of hours of light received, but when a plant will Rower-before or after a critical day length

1. Ashort-day plant flowers when the day length is less than a certain critical length Day lengths in EXCES of this critical point will keep the short-day plant vegetative. The so-called critical day length differs with different species Some examples of short-day plants are Niration

(Maryland Mammoth) Xan pemain (cocklebur).

and Glyvu (Biloxi soybean).

2. A lowe-day plow flowers after a critical

day length is exceeded. Again, this critical day length differs from species to species. Some examples of long-day plants are Spinarea elevarea (spinach). Bera rulgaris

importance of dark period Plants under normal conditions are subjocted to a 24 hour cycle of light and dark ness. Early workers on photoperiodism also used a 24 hour cycle, thus emulating the natural condition. It soon became apparent that a more sophisticated analysis of photoperiodism could be obtained by changing the normal

cycle, for example, by following an 8 hour light period with an & bour dark period or following a 16 hour lobt period with a 16 hour dark period. Subjection of long and short-day plants to cycles other than 24 hours convincingly demonstrated that flowering in plats is more of a response to the dark period han to the right. That is, short-day plants flower when a certain critical dark period is exceeded, and long-day plants Hower when the duration of the dark period is less than a critical value.

The importance of the dark period on the Flowering Response

Although controlling effects of photo- periods on flowering were observed before the twentieth century, the first good experi- mental evidence supporting this concert was presented during the carly years of this century, Tournois (1912) attempted to answer the question of why hemp flowers

Although relatively rare, there are some plants that require a long photoperiod, Succeeded by a short photoperiod, to flower. Also, a relatively few plants are induced to flower when short photoperiods are followed by long photoperiods. The above plants, reguiring a long-short-day sequence or a short-long-day sequence to

short period.

Quantitative effect of lielis duration and intensity on floral initiative by Biloxiwaybe on a photoinductive cyde. Note that no flowers are produed with lightTensities wider

10 fic and that the greater number of flowers are produced with the longer phe period. (After KC Hamer. 1910. Botan Gax. 1011 66.)

the most sensitive, while the very young armature leaves are much less sensitive to photoperiodic induction (Hammy, 1954).

Surprisingly enough, mature Jenves also seem capable of neutralizing the flower promoting effect of a photoperiodic stimulus. That is, when a photoinduced leal or branch is grafted to a plant receiving a honductive cycle, mature leaves prevent on the receptor plant antagonize progress toward the lowering response. Defoliation of the receptor plant climinates the antagonism.

It must be understood that the formation of flowers by a plant is an all or nothing affair with respect to photoperiodism. Once a plant has received the minimum number of photoinductive cycles, it will flower, even if returned to noninductive cycles,

Partial induction has been observed in short-day plants. The short-day plant Ima s lalam , for example, requires only three photoinductive cycles for floral bud initiation. For these bus to form flowers, however, more than eight photoinductive cycles are necessary (Krisme martly Nude, 1967; New and Krishnary, 1967).

Partial induction may also be obtained in the long-day plants. The long-day plant, Plawa lanceolata, needs 25 photoinductive cycles for 100% inflorescence formation. If the plant is given 10 photoinductive cycles and then subjected to a noninductive cycle, it will not flower. However, when the plant is returned to photoinductive cycle, only 15 cycles are needed to produce 100% inflorescence (Hilm , 1962). For-mation of Aoral primordia by the aquatic plant Lim gibba requires a minimum of one long day. However, at least six long days are required to obtain mature flowers, long days apparently being required for the

early stages of tower development in this plant (Cleland and Brices, 1967). Similar results have been obtained by Naylor (1941) and Lang and Melchers (1947) with other long-dny plants.

The implication is that some factor involved in the flowering response is accumulated during the inductive cycle. in some plants (eg. Xa l) cnough is accumulated after only one cycle to promot flowering. In other plants more than one inductive cycle is needed. In long day plants, the noninductive cycle does not appear to modify the effects of a previous exposure to an inductive cycle. The noninductive cycle in short-day plants, however, appears to be inhibitory, Schwabe (1959) has shown this effect in several shortday pants by alternating inductive and noninductive cycles. The noninductive cycle inhibits the effect of the previous inductive cycle.

Knott (1931) demonstrated that in spinach, a long-day plant, the leaves are the receptors of the photoperiodic stimulus. In addition, he postulated that something is produced in the leaves in response to a photoinductive cycle and then translocated to the apical tip, causing the initiation of Aaral primordia.

Evidence for leaves being the organs of perception in the flowering response to photoinductive cycles is overwhelming In many cases, giving photoinductive cycles to a single leaf, while the rest of the plant is on a noninductive cycle, is sufficient to case flowering. For example, if a single Jeaf of Xanthi is exposed to short photoperiods, while the rest of the plant receives long photoperiods, flowers are formed

Grafting of photoiduced leaves from olie plant to another plant on a neninductive cycle has been shown to promote flowering on the receptor plant (Heiner of al.192; Naylor, 1953). Before grafting the photoinduced leaves, the receptor plants are first defoliated to climinate any influence of the noninduced leaves.

A minimum amount of caftist appears necessary for flowering to occur (Parhey aud Parol, 1952; Heldent, 1956). The developmental stage of the leaf is also important in regard to sensitivity to photo periodic induction. For example, partially mature Xant leaves have been found

Presence of a floral hormone The flowering factor produced in photoinduced leaves is apparently transported with relative case in the plant. One inventi gator, studying the floral hormone in Chryshme, demonstrated the diffusion of this hormone across an incomplete graft union separated by a water gap (Mosloker, 1937). However, this experiment lias DEVCE been successfully repeated (Girlsvi, 1949; Moslobor, 1919). Cajlachjan, who has performed numerous experiments demonstrating the probable existence of a floral hormone, has given the name florigo to the. as yet, isolated hormone (1934). There is some indication that florigen may be an is peeneidoras croid-like compound (Rise of al. 1966; Power of al., 1963; Lang, 7905).

Perhaps the most dramatic demonstra tion of the case with which the floral ho mone is translocated has been observed in two-branched Xaw plants grafted in series. If the end brand of a series of plants is given a photoinductive cycle, it will cause flowering in all six plants in a chainlike reaction (see review by Naylor (1961) See Figure 2-5.)

Equally as dramatic were the experimeats of Zeevaart (1954), in which he grafted long day plants to short-day plants and view. When the long-day plant, Sed semile, was grafted to the short

Perception of the Photoperiodic

Floral Hormone A good deal of the early work on photoperiodism was aimed at establishing which part of the plant receives the photoperiodic stimulus. The organs of the plant receiving the most attention were the leaves and buds.

Transaction of the fallorme, One bunch of a two-hrched and plant, gifted

of five oth Xullas, was given photoinductive cycle. The second hanch of the i lmt d the other five phare kept on a maphotoinductive cycle. All plants fowered

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